



# Prospects for the future of pink salmon in three oceans: From the native Pacific to the novel Arctic and Atlantic

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## Abstract

While populations of other migratory salmonids suffer in the Anthropocene, pink salmon (*Oncorhynchus gorbusca* Salmonidae) are thriving, and their distribution is expanding both within their natural range and in the Atlantic and Arctic following introduction of the species to the White Sea in the 1950s. Pink salmon are now rapidly spreading in Europe and even across the ocean to North America. Large numbers of pink salmon breed in Norwegian rivers and small numbers of individuals have been captured throughout the North Atlantic since 2017. Although little is known about the biology and ecology of the pink salmon in its novel distribution, the impacts of the species' introduction are potentially highly significant for native species and watershed productivity. Contrasts between pink salmon in the native and extended ranges will be key to navigating management strategies for Atlantic nations where the pink salmon is entrenching itself among the fish fauna, posing potential threats to native fish communities. One key conclusion of this paper is that the species' heritable traits are rapidly selected and drive local adaptation and evolution. Within the Atlantic region, this may facilitate further establishment and spread. The invasion of pink salmon in the Atlantic basin is ultimately a massive ecological experiment and one of the first examples of a major faunal change in the North Atlantic Ocean that is already undergoing rapid changes due to other anthropogenic stressors. New research is urgently needed to understand the role and potential future impacts of pink salmon in Atlantic ecosystems.

## KEYWORDS

Atlantification, biological invasions, climate adaptation, Pacific Ocean, regime shift

## 1 | INTRODUCTION

Biological invasions are considered a top threat to biodiversity on a global scale (Simberloff et al., 2013). Species that escape their

native range and become established in a new area become competitors, predators, prey or parasites of native species and can cause regime shifts that contribute to the collapse of valuable native species or even ecosystems (Didham et al., 2005). Research

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on marine invasive species in the North Atlantic basin has mostly focused on benthic species such as Pacific oyster (*Crassostrea gigas* Ostreidae) or more recently sea vomit (*Didemnum vexillum* Didemnidae; Schmidt et al., 2008). In Arctic regions of the Atlantic Ocean and Barents Sea, impacts of species such as the red king crab (*Paralithodes camtschaticus* Lithodidae) have been debated, and this crab now supports valuable fisheries making extirpation of the invader a complex social issue (Lorentzen et al., 2018). Successful invasions by marine fish species have been rare in temperate and Arctic seas, but in the western Atlantic Ocean, the Indopacific lionfish (*Pterois volitans* Scorpaenidae) has caused declines of native coral reef fish (Green et al., 2012), exemplifying the disruptive potential of invasion in marine ecosystems. Now, anadromous pink salmon (*Oncorhynchus gorbuscha* Salmonidae) populations have been firmly established in Northwest Russia after deliberate releases, and colonists have spread from there to Norway and other countries around the North Atlantic Ocean (Armstrong et al., 2018; Eliassen & Johannesen, 2021; Millane et al., 2019; Nielsen et al., 2020; Sandlund et al., 2019). Numbers of detected pink salmon have been highest in Finnmark in northern Norway, with local people demanding resources to mitigate what they perceive as a major deterioration of the ecosystem services provided by the fishing of highly valued native species. Concerns further strengthened when the largest pink salmon run ever to the region occurred in 2021, with catches exceeding those of native Atlantic salmon (*Salmo salar* Salmonidae) in Norwegian rivers (<https://www.ssb.no/jord-skog-jakt-og-fiskeri/fiske-og-fangst/statistikk/sjofiske-etter-laks-og-sjoaure>, Diaz Pauli et al., 2023).

Pink salmon is a migratory, anadromous salmonid with a mostly fixed 2-year life cycle (Heard, 1991). Pink salmon lay eggs in river or intertidal (Helle et al., 1964) gravel. Individuals from coastal populations have seawater tolerance from early in life (Beacham, 1992). Spawning takes place from mid-July to late October, and eggs commonly hatch from late December to late February in the species native range in the Pacific region (Scott & Crossman, 1973). Alevins remain in the gravel until the yolk sac is absorbed usually in April–May, but may be as early as late February. After emergence from the gravel, they migrate quickly to the ocean. The diminutive smolts of pink salmon (3–6 cm; Grant et al., 2009) enter the ocean in very high numbers and are a major potential resource from the freshwater environment to marine predators. Pink salmon migrate to the open sea but may first stay in inshore waters for up to several months (Scott & Crossman, 1973). In the Pacific Ocean, pink salmon have high dietary overlap with other Pacific salmonids (Johnson & Schindler, 2009), growing quickly for about a year before returning to coastal zones and migrating back to spawn in rivers where they all die post-spawning. The carcasses of pink salmon populate riverbanks where they feed scavengers and their corporal nutrients decompose, which fertilizes streams and the surrounding forest and promotes growth of stream invertebrates that serve as food for the many Pacific salmonid species occurring in Pacific ecosystems (Nelson & Reynolds, 2015) and cascading ecosystem impacts (Walsh et al., 2020).

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Pink salmon have recently reached record-high abundances in the Pacific Ocean, based on data collected since 1925. Fish in the ocean primarily originate from wild reproduction, although a modest proportion of the animals result from hatchery stocking programmes mostly in the Western Pacific area (Ruggerone & Irvine, 2018). The extremely high abundance of the species in the Pacific Ocean has dramatic consequences for the forage base and competing salmonid species. Ruggerone and Nielsen (2004) revealed striking biennial correlations between pink salmon abundance and reduced production of other Pacific salmonids. Effects of competition for marine prey among pink salmon and seabirds have also been proposed, as associations between mass mortalities in birds migrating between the northern and southern hemisphere and pink salmon abundance have been demonstrated (Springer et al., 2018).

Despite their newfound preponderance in the rivers of northern Norway and concerns that the species could spread further throughout the country, to other European countries, and even across the Atlantic to North America, the ecology of pink salmon in the Atlantic

and Arctic is still relatively unknown (Hindar et al., 2020). The trajectory of pink salmon in the North Atlantic in the coming years is a matter of speculation and modelling, but it is timely to prepare as though pink salmon will further establish and become a more prominent fixture of the marine and freshwater ecosystems in the Atlantic Ocean and Barents Sea area. Knowledge about the potential impacts of this species on native ecosystems is lacking, limiting the potential for informed preparation and action by management and local stakeholders. We endeavour to synthesize literature on pink salmon during its different life stages, from its natural range in the Pacific, combined with the growing knowledge about invasive pink salmon in the Atlantic Ocean and Barents Sea area, with the aim to better understand the potential threats posed by invasive pink salmon in the Atlantic and Arctic. This review lists concerns about the potential impacts of pink salmon on its new ecosystems and discusses the evidence and, where relevant, research needs to support effective measures.

## 2 | SYNTHESIZING PINK SALMON KNOWLEDGE BETWEEN PACIFIC AND ATLANTIC

### 2.1 | Juveniles in freshwater

#### 2.1.1 | Hatching and gravel emergence time

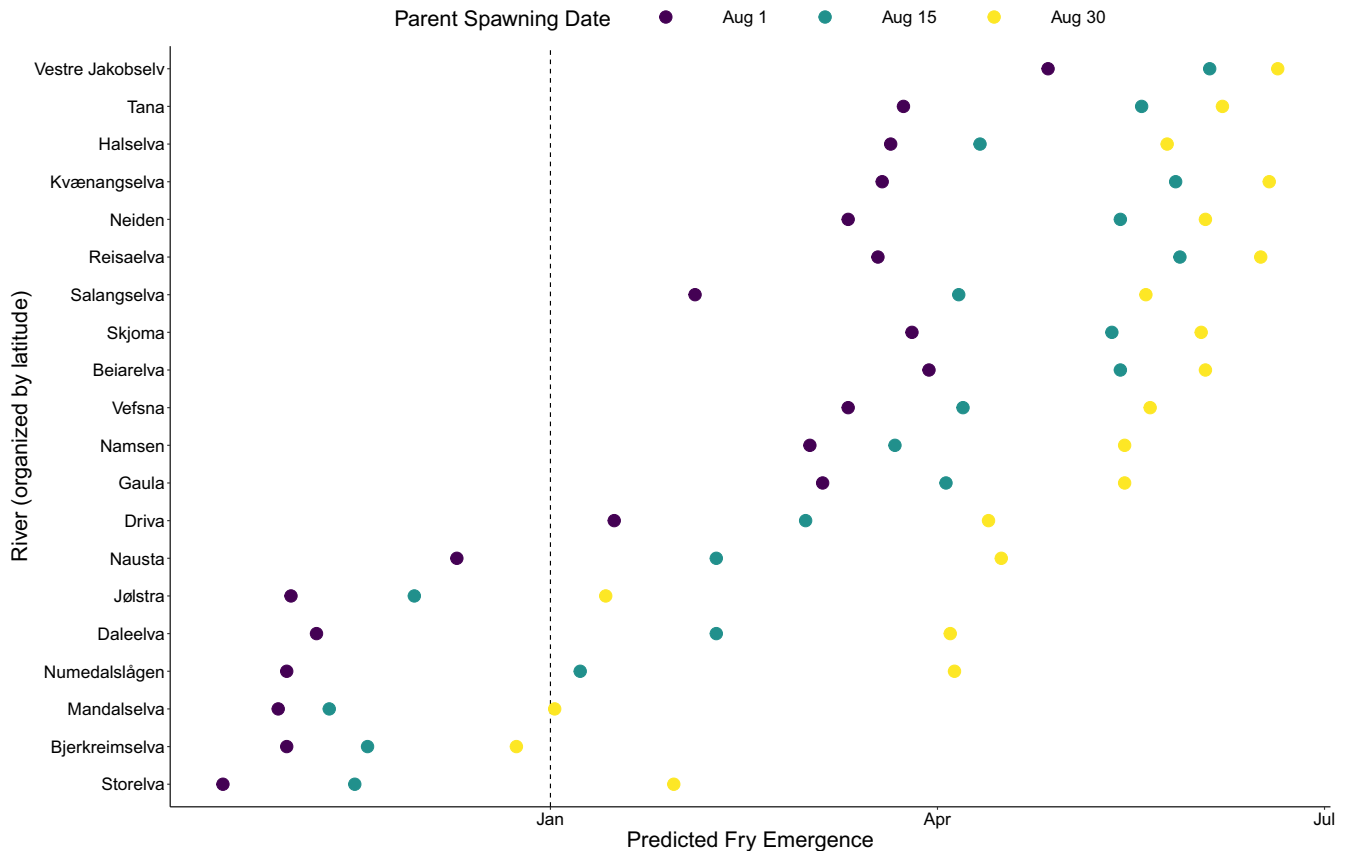
Native pink salmon eggs are laid in the gravel of rivers (and also estuaries!) in the Pacific region during the autumn, hatching the following spring. The hatching time of the eggs depends on when the eggs are laid and the degree days that they accumulate in the interstitial gravel, which in turn depends on latitude (Erkinaro et al., 2022). In the Pacific, pink salmon spawning from August to October precedes that of the other salmonids and there is variation within individuals when they spawn. This is critical, because studies in the native range have demonstrated that early- and late-run spawners produce offspring with different hatching times (Murray & McPhail, 1988; Taylor, 1980), and hatching time is hypothesized to be a critical variable influencing invasiveness in the Atlantic realm.

Pink salmon spawning has been observed in Atlantic rivers in August–September, which is early compared to the native Atlantic salmon and anadromous brown trout (*Salmo trutta* Salmonidae) that spawn October–December in most cases (Anon, 2022a, 2022b; Sandlund et al., 2019; Sørvik, 2022; Vistnes, 2017). However, there may be some overlap in the spawning period between pink salmon and anadromous Arctic charr (*Salvelinus alpinus* Salmonidae), which mainly spawn in September (Anon, 2022a, 2022b). In northern rivers, brown trout may also commence spawning from early September, thus overlapping with late spawners of pink salmon. There is an expectation that pink salmon eggs in southern Norway and Scotland hatch in the fall or winter and offspring are exposed to harsh winter conditions (Armstrong et al., 2018). Erkinaro et al. (2022) found that pink salmon eggs from the subarctic River Tana/Teno hatched

in mid-October and would either have to delay emergence from the gravel, survive the winter in the river, or migrate directly to sea at a suboptimal time. Large variation among rivers according to whether they are relatively warm or cold during the autumn and winter results in large variation in the timing of gravel emergence. Many rivers in southern Norway have expected swim-up timing (i.e. when the yolk sac is fully consumed) for pink salmon fry in the spring if spawning occurs in late August according to models based on daily water temperature, but delayed spawning can greatly postpone the gravel emergence timing (Figure 1). Hence, the expectation that pink salmon will not successfully reproduce due to premature hatching and swim-up in southern Norway and other European rivers (Armstrong et al., 2018) may be faulty and shows the limitations of predictions when we know little about plasticity and evolution of this White Sea origin stock in the Atlantic region. In support of plasticity, pink salmon smolts were recorded in Scottish rivers in March 2022, and the authors concluded that this provides evidence of successful spawning and rearing from the 2021 spawning cohort, completion of the freshwater phase of the life cycle, indicating the possibility for potential long-term establishment of a pink salmon population in the United Kingdom (Skóra et al., 2023).

Hatching early means pink salmon fry either have an extended period in the gravel to avoid predation and harsh conditions as they await suitable outmigration temperature and flow, or alternatively emerging from the gravel to initiate premature migration to the ocean or attempt to feed and avoid predation in freshwater during the harsh winter. Premature migration to the ocean has not been recorded, so most likely pink salmon fry wait in the gravel for better emergence conditions, perhaps minimizing yolk consumption. Delayed emergence has been observed for other populations of pink salmon experiencing prolonged near-freezing temperatures (Gordeeva & Salmenkova, 2011). Indeed, large numbers of pink salmon smolts with and without remnants of the yolk sac were observed in 19 North Norwegian rivers in the spring and early summer (late April–early July) during 2018–2022 (Hansen & Monsen, 2022; Muladal, 2018; Muladal & og Fagard, 2020, 2022). Any plasticity that exists in the spawning times or developmental rates in the wild may help the juveniles suspend emergence and migration timing to account for variable thermal regimes. The scope of this plasticity needs to be documented and is an important future research topic in the areas where the species is invading. The egg development is fast when the river temperatures are still high early in the autumn, so a few days difference in timing of spawning may result in a large difference in timing of swim-up in the spring. Hence, a relatively small difference in spawning time of parents may have a large impact on the timing of gravel emergence and swim-up of their offspring (Figure 1).

Pink salmon are often reported to move directly to sea after hatching (Heard, 1991) but are probably more strategic than that. Arrival of pink smolts to the sea is reported from March to May (Duffy et al., 2005; Simenstad et al., 1982; Skud, 1955) in the species' Pacific distribution and into June from the White Sea populations (Kirillov et al., 2018; Pavlov et al., 2015; Robins et al., 2005; Varnavsky et al., 1992; Veselov et al., 2016). Pink salmon smolts have been found



**FIGURE 1** Predicted timing of fry emergence from gravel (swim-up, when yolk sac is used up) for pink salmon hatched in rivers in Norway. Estimates are provided for spawning times at three different intervals in August, a commonly observed spawning occurrence in Norwegian rivers. Rivers are sorted from south (bottom) to north (top) by latitude. The vertical line indicates January 1, that is a new year.

in the lower part of Norwegian Kongsfjordelva from mid-May until early July (H. Vistnes, pers. comm.); apparently, these individuals are growing and feeding, which merits more detailed investigations to determine whether they are delaying migration to sea in favour of feeding in the estuary. Productive feeding places are clearly important for pink salmon, with areas such as lakes providing foraging grounds that smolts spend time in rather than moving right to sea. Many rivers in Norway have exorheic lakes where native salmonid parr rear and where pink salmon fry may feed before going to the ocean, and this too merits investigation (Lennox, Pulg, et al., 2021).

Timing of spawning clearly has an enormous impact on the adaptation of pink salmon to Atlantic conditions. If there is variation in spawning times and there is sufficiently strong selection toward late autumn or spring spawners, then the species may be able to find success in Atlantic rivers simply by adjusting spawning time. Timing of spawning is a trait with large inter-individual variation with a likely genetic basis among salmonids (Smoker et al., 1998; for pink salmon; Heggberget, 1988 for Atlantic salmon). Indeed, the pink salmon of the population in Northwest Russia have different phenotypes than the donor population in eastern Russia, suggesting rapid evolution and adaptation (Gordeeva et al., 2015). Correspondingly, there are anecdotal observations of a progressively later spawning timing for autumn spawners among some pink salmon in recent years in Norway and Russia, as late as early October. Since these populations

are the putative source of the new colonists entering the Atlantic Ocean, this seems to indicate that the species has already begun adapting to regional conditions. Consequently, we anticipate a later hatching time of their offspring and potentially more favourable conditions encountered at sea, leading to increased abundance and greater extent of establishment of pink salmon in the Atlantic.

### 2.1.2 | Feeding in freshwater

The degree to which pink salmon feed in freshwater is somewhat ambiguous from literature emanating from both the Pacific and Atlantic regions; that they are able to feed in freshwater post-emergence but it seems that this is context dependent (e.g. Robins et al., 2005). When pink salmon hatch at about 3 cm in length, they have a yolk sac that they will deplete before needing to feed exogenously. Earlier hatching in cold conditions probably leads to slower consumption of yolk due to the slower metabolic demands at low temperatures. These early risers most likely shelter in the gravel, minimizing metabolism and slowly subsisting on the yolk. It is generally held that pink salmon do not migrate until the yolk is depleted, so whether they hatch early, during winter, or late, during spring, they will have to decide once the yolk is gone whether to immediately migrate or feed a bit in freshwater. In a Russian

river draining to the White Sea, Veselov et al. (2016) observed that 84% of pink salmon smolts that they collected during the month of May had commenced feeding, and 100% of those captured in June had done so.

Evidently, at some sites pink salmon can linger in rivers after hatching and the timing of their freshwater residency will determine their relationship to the native salmonids; they may compete for invertebrate food or territory, they may eat eggs or fry of native salmonids, or they could be prey for larger salmonid parr. In the Pacific region, native fish were found to consume large numbers of riverine pink salmon fry (Schoen et al., 2022); native salmonids in Norwegian rivers may also capitalize on the emergence of these fry in winter and spring when food is relatively scarce. However, aggression ("contest competition") by pink salmon fry may exclude native species and be an agonistic interaction, or native fry may simply be displaced and crowded out if pink salmon fry occur in large numbers ("exploitative competition"). To date, experimental studies of potential contest competitive interactions among juvenile Atlantic native salmonid species, and juvenile Pacific salmonids have not included pink salmon (e.g. Fausch, 1988; Gibson, 1981; Houde et al., 2017), perhaps because this was assumed to be unlikely to occur. A re-examination of this assumption is now due. Competition for these spaces may be stressful for the native fish even without direct interaction, resulting in early density-dependent mortality owing to space limitations. How long pink salmon fry stay in Atlantic rivers is unknown, but their large numbers could deplete some of the overall salmonid food supply especially if they linger for long periods during productive months in the river. Given the short length of most European rivers, pink salmon can probably complete the river migration rapidly, shrinking the window for potential feeding in most rivers and perhaps mitigating the potential for competition with native counterparts.

### 2.1.3 | Onset of smolt migration

Various estimates have been made on the timing of pink salmon arrival to Pacific estuaries, generally showing that they arrive between March and May with a putative peak in April (Duffy et al., 2005; Skud, 1955; Simenstad et al., 1982). However, the pink salmon migration can extend later into June and beyond (Pavlov et al., 2015; Robins et al., 2005; Varnavsky et al., 1992) and is probably a function of time of swim-up, river length, presence of lakes, temperature, flow and other factors. In the native range, the run of pink salmon may be bimodal and driven by temporal separation in the hatching times for offspring of early and late spawners (Taylor, 1980). Kirillov et al. (2018) found that pink fry migration peaked at river temperatures of 5–10°C at about 50° latitude. Veselov et al. (2016) investigated the invasive Russian population of the Indera River and observed migration from 1.5 to 10.5°C in the month of May. In northern Norway, observations of pink salmon fry suggest they are migrating around the middle of May but also later in some streams (Bjerknes, 1977, and as described above). Climate change

is advancing the timing of spawning, accelerating egg development, and resulting in earlier outmigration times of pink salmon in their native range that may contribute to mismatches with prey abundance and productivity there (Taylor, 2008).

Pink salmon smolts are small and may be subject to or reliant to some extent upon river discharges to carry them out to sea (Duffy et al., 2005), although they seem to swim actively into the currents (Pavlov et al., 2019) and may be actively migrating in the downstream flows at night before concealing themselves in gravel during daytime (Neave, 1955; Yamada et al., 2022). Investigations from the Pacific have demonstrated that timing of emergence may affect residency time in estuaries; the existence and maintenance of this variation may be an important lever for natural selection to act on pink salmon in Europe, depending on the heritability of emergence timing.

## 2.2 | Post-smolts and early marine phase

### 2.2.1 | Estuary residence

Pink salmon enter estuaries in spring or summer as small larvae that must feed and grow to survive. Tang et al. (2011) demonstrated a preference for upper layers of the water column (<1 m), where currents are fastest and transport out to the open sea should be swiftest. It was also shown that the pink salmon smolts moved deeper as they acclimated to seawater, and individual physiological preparedness for marine entry may therefore in whole or in part determine the duration of estuary residence for individuals. Preparedness for seawater is river temperature dependent with an optimum around 9°C (Varnavsky et al., 1993). Pink salmon are generally thought to make rapid transitions away from estuaries to feed in the open sea. However, new isotopic methods are demonstrating that there is considerable variation in the estuary residence times and that pink salmon can remain near their home river mouths for weeks after migrating (Moore et al., 2016) including in tidal marsh areas that require daily movements in and out to avoid desiccation (Levy & Northcote, 1982). Early migrating pink salmon that arrive first in estuaries may have longer residence times there than later-running counterparts (Mortensen et al., 2000). As climate change advances freshwater migrations to earlier in the year, more pink salmon may find themselves in colder estuaries and must delay seaward migration with prolonged estuary residence times (Taylor, 2008). Estuaries and coastal areas are very variable in terms of hydrology, other environmental conditions (e.g. salinities, oxygen concentration, turbidity) and ecology, which may be expected to result in large variation in pink salmon juvenile behaviour in these areas.

### 2.2.2 | Offshore migration and interactions with prey, predators and parasites

Once pink salmon depart the estuary, growth may slow for a period while they travel to find higher quality food or switch to more



energy-efficient food sources, evidence for which has been observed in scale analyses (Heard, 1991; Kaev & Zhivotovsky, 2017; Myers, 1994; Paulsen et al., 2022). The early marine period of pink salmon in the Pacific Ocean may determine the ultimate abundance of returning fish, but the size of adults returning may be more impacted by environmental and growth conditions in the later marine period when they are further offshore (Kaev & Irvine, 2016; Paulsen et al., 2022). However, smolt-to-adult recruitment is generally low in the Pacific basin rivers, estimated to be 0.7%–5.2% in the eastern Pacific (Hunter, 1959) and 1.25%–7.03% in the western Pacific (Kaev & Rudnev, 2007). Favourable conditions during the migration will facilitate growth and survival (Moss et al., 2005), which has evidently occurred in the Norwegian and Barents seas since the population of pinks exploded in Norway in 2017. Hindcasting exercises may be helpful to understand what confluence of biological and oceanographic factors converged in this period that could explain the sudden preponderance of pink salmon in the Atlantic region. Similar to other marine species in this area with passive larvae (e.g. Norwegian spring-spawning herring [*Clupea harrangus* Clupeidae], capelin [*Mallotus villosus* Osmeridae], haddock [*Melanogrammus aeglefinus* Gadidae], cod [*Gadus morhua* Gadidae]), advection of the small pink salmon smolts is hypothesized to be an important determinant of the ultimate marine range. Marine fish larvae spawned off the coast of Norway are quickly transported north- and eastward with the water currents, resulting in a large proportion of the zero-group fish located in the eastern Barents Sea during the autumn (ICES, 2021). It is expected that pink salmon will find themselves in similar areas of the Barents Sea if they follow similar dynamics, which matches empirical observations (Bjerknes & Waag, 1980; Diaz Pauli et al., 2023). The surface temperature in the eastern Barents Sea has warmed in recent years, with autumn temperatures in 2020 more than 3°C higher than the average for the period 1981–2010 (ICES, 2021). Ocean warming in the north Atlantic Ocean and Arctic is seen as a key factor driving increased abundance of pink salmon in the Atlantic region (Hindar et al., 2020).

The diet of pink salmon in the Atlantic Ocean during the first year of sea is little studied, but they are generally opportunistic generalists (Andrews et al., 2009; Diaz Pauli et al., 2023). Given their size, it makes sense that they are feeding mostly on pelagic amphipods and copepods (Heard, 1991). There is likely significant variation in foraging success early in the migration, when most of the diet consists of relatively low energy prey dominated by small zooplankton (Beauchamp, 2009). Boldt and Haldorson (2002) estimated that the diminutive but abundant pink salmon can consume a large proportion of total copepod and amphipod populations in estuaries, representing a major predator and energy conduit to the Pacific Ocean. The immense abundance of pink salmon in the Pacific and their intensive feeding has been observed to drive the Pacific ecosystem, with impacts on survival of other salmonids and even whales (Ruggerone & Irvine, 2018; Ruggerone et al., 2019). Such impacts are unlikely in the Atlantic at least at present where rivers are much smaller and the biomass of pink salmon smolts is orders of magnitude lesser. As they grow, the diet shifts to include more fish

and squid and they continue feeding until they return to coasts and enter rivers (Diaz Pauli et al., 2023). Predation by pink salmon around coasts, sounds and fjords as they return in the Pacific is considered a factor regulating abundance of key forage fish species such as herring (Sturdevant et al., 2013). They may even feed on the smolts of pink salmon as they exit rivers, potentially driving odd-even year dynamics characteristic of the species (Krkošek et al., 2011). Diets of pink salmon returning to coasts in the North Atlantic should be analysed for the presence of native salmonid smolts.

## 2.3 | Return migration

### 2.3.1 | Energetics and Homing

In every waterbody except for the Laurentian Great Lakes (Kennedy et al., 2005), pink salmon return to coasts after about 12–14 months in the ocean to migrate into rivers and spawn. Like other salmonids, pink salmon have a magnetic map that they can use to orient from the ocean towards home rivers (Putman et al., 2020). Pink salmon have mainly entered Norwegian rivers from late June to mid-August, and Sandlund et al. (2019) and Diaz Pauli et al. (2023) identified no relationship between timing of entry and latitude. Pink salmon have also been observed entering rivers as late as September (Anon, 2022a, 2022b; Diaz Pauli et al., 2023; Vistnes, 2017 Sørvik, 2022). Once pink salmon enter a river, they may still return to the estuary before making a final spawning migration (Morita, 2022). Although pink salmon have historically been thought to be relatively poor swimmers (Heard, 1991), adult pink salmon are in fact strong and energetically efficient migrators. Laboratory swim flume trials revealed that males can attain instantaneous swim speeds >2m/s and females up to 1.5m/s (Standen et al., 2002). Results from EMG telemetry tracking in the Fraser River showed that pink salmon generally swam at slower speeds than their maximum capacity averaging 1.1m/s with somewhat faster speeds (up to 1.8m/s) elicited in areas with faster and more complex flows (Standen et al., 2002). Hinch et al. (2002) found that their swimming pace was steadier and less variable than co-migrating sockeye salmon (*Oncorhynchus nerka* Salmonidae) in the Fraser River which translates into reach-specific energetic costs for pink salmon, estimated from EMG telemetry, being similar to, or less than, that of sockeye salmon (Standen et al., 2002). Direct energy assessments have been made on individual adult pink salmon at the start of the freshwater spawning migration, the end of migration before spawning, and immediately after spawning, for both a long distance (~500km) and short distance (~50km) upriver migrating population in the Fraser River (Crossin et al., 2003). Curiously, the investigators found no energetic or morphological differences either at river entry or upon arrival at spawning areas regardless of the level of migratory difficulty. In comparison to co-migrating sockeye salmon, pink salmon began upriver migration with significantly smaller somatic energy reserves, yet arrived at spawning

grounds and completed spawning with similar energy reserves to sockeye (Crossin et al., 2003). Presumably, pink salmon were able to minimize absolute movement and activity costs by seeking out migratory paths of least resistance (Hinch et al. 2002).

Cardiorespiratory measurements demonstrate an elite level of athleticism in pink salmon in comparison with several other Pacific salmon species, with pink salmon having superior maximum heart rates, cardiac output, cardiac stroke volume, and peak oxygen consumption rates (Clark et al., 2011). Some populations of pink salmon currently migrate several hundred km up the Fraser River in British Columbia including several reaches with rapids and steep gradients, thus they would be expected to pass an array of challenging river reaches in the shorter and often less steep Atlantic rivers. Pink salmon are also the superior species of Pacific salmon in terms of adult aerobic scope and thermal tolerance, having an optimum temperature in the Fraser River of 21 C (Clark et al., 2011) suggesting they will be able to cope better than other salmonid species in rivers warming due to climate change.

Unlike other Pacific salmon, pink salmon have relatively low affinity for natal streams and their odours, likely enhancing the species ability to expand its range (Ueda, 2012). Over the past several decades, Fraser River pink salmon have expanded their range considerably upriver (100s km; S. G. Hinch, pers comm.). Another indication of their lower affinity for olfactory cues comes from a recent study examining disturbance cues in Y-maze experiments. Migratory fish species often exhibit increased cortisol levels and are exposed to numerous stressors during their migrations, which trigger the release of chemical disturbance cues. Bett et al. (2016) found that while sockeye salmon avoided the odour of disturbed conspecifics, pink salmon did not. Homing precision of pink salmon seems to be somewhat less than for other anadromous salmonids (Hendry & Stearns, 2003) but varies among studies. Coded wire tag studies in the Prince William Sound in Alaska gave a straying rate of 34.1% (Habicht et al., 1998), whereas two studies in Southeast Alaska employing thermal marks, CWT and fin clips, suggested average straying rates at 5.1% (Thedinga et al., 2000) and 6.3% (Mortensen et al., 2002), respectively, with modest variation among experiments (see Appendix 1, Evolution Illuminated, Hendry & Stearns, 2003). By contrast, wild Atlantic salmon straying rates within the species natural range average 10.1%, with point estimates up to 20% (Keefer & Caudill, 2014). In line with this, pink salmon also show less genetic variation between rivers than other salmonids, even when studies are carried out across large spatial scales (Appendix 2, Evolution Illuminated, Hendry & Stearns, 2003). Because of their strict 2-year life cycle, pink salmon may show larger genetic differences between odd- and even-year populations in the same river, than among rivers within year class (Tarpey et al., 2018). Continental genetic differences are still larger than the difference between year classes within the Asian and the North American continent (Tarpey et al., 2018).

The 2017 invasion by pink salmon into many rivers of northern and southern Europe, Iceland, and even Greenland and the east coast Canada (some of which were >5000 km away from the White Sea) demonstrates the enormous potential for spreading of

the species to all of the North Atlantic Ocean, and also into the Arctic Ocean. A risk assessment in Norway suggested that pink salmon are likely to become a northern circumpolar species (Hindar et al., 2020). The same conclusion seems to have been reached by Nielsen et al. (2013). These predictions are supported by swim performance and cardiorespiratory studies (Clark et al., 2011). However, it is important to note that the dramatic changes to climate supporting such a range expansion of pink salmon will also affect many other species, such that the North Atlantic and Arctic Oceans will be greatly changed by more than just the establishment of pink salmon but a wholesale regime shift. It is far from clear that this will in the long term necessarily favour pink salmon. For example, a drastically changed predator field could suppress the species.

### 2.3.2 | Parasites, opportunists and pathogens in pink salmon in the Pacific Ocean and North Atlantic

The parasite fauna of pink salmon in the North Atlantic and Barents Sea reflects the food web that the species has become a part of and the environment they live in. The parasites described often have low host specificity, which means they are generalists and are thus often also present in native salmonids (Fjær, 2019; Rullestad, 2021). Some of the parasites have complex life cycles (transmitted trophically) and multiple intermediate hosts, where not only the abundance of infected salmonids (native and introduced) will determine the impact on the ecosystem. For directly transmitted parasites, pink salmon can be a new reservoir of generalist pathogens that can interact with native wild and cultivated farmed fish. In contrast to Atlantic salmon, pink salmon has a clear and strong immune response to salmon lice (*Lepeophtheirus salmonis* Caligidae) during early marine life stages (Sutherland et al., 2014). One should expect that salmon lice infestation pressure that is detrimental to Atlantic salmon (e.g. Johnsen et al., 2021; Stige et al., 2022) may be less problematic for pink salmon, giving a competitive advantage to pink salmon compared to Atlantic salmon in environmental conditions that promote lice promulgation. Pink salmon are not, however, completely immune to salmon lice as studies from the north Pacific have shown that populations of pink salmon can be negatively impacted by salmon lice similar to Atlantic salmon (e.g. Vollset et al., 2023), with reduced returns in years with high infestation pressure during their smolt year (e.g. Krkošek & Hilborn, 2011). The immunity to salmon lice seems to disappear when pink salmon gets closer to maturation. The consequence is that returning adult pink salmon may be an important host and vector for salmon lice during their return. Nevertheless, lower vulnerability of pink salmon to lice may provide a distinct advantage to pink salmon versus the native species that are greatly burdened by lice in many parts of Norway due to intensive Atlantic salmon farming.

Pathogen screening of 27 pink salmon in Gulf of Alaska (GoA) during the winter of 2019 demonstrated that they are carriers of

several opportunistic and pathogenic species (Deeg et al., 2022). The opportunistic bacterium *Candidatus Branchiomonas cysticola* seems to be ubiquitous and highly prevalent in pink salmon in the Pacific and native salmonids in Norway (Garseth, Florø-Larsen, et al., 2020; Gåsnes et al., 2019; Lennox et al., 2020). The bacterium has also been detected in pink salmon in Norway (Fjær, 2019). Furthermore, *Parvicapsula pseudobranchicola* Parvicapsulidae and *Desmozoon lepeophtherii* Enterocytozoonidae (synonymous *Paranucleospora theridio*) were prevalent in Alaskan pink salmon and also in Norway (Fjær, 2019; Garseth, Florø-Larsen, et al., 2020). *Ichthyophonus hoferi* Ichthyophonidae is referred to as an important pathogen of pink salmon in the Pacific Ocean (Deeg et al., 2022). This parasite is mainly transmitted trophically (by ingesting infected prey). *Ichthyophonus* sp. was recently detected by histopathological investigation of organs from a moribund pink salmon captured in a Norwegian river in 2021 (Garseth et al., 2023).

Pink salmon may be susceptible to many of the same microparasites and pathogens (virus, bacteria, fungi, protists, protozoans) that cause disease in salmonids native to the North Atlantic. A main aim of some studies has thus been to investigate the presence of viruses and bacteria that cause disease in the aquaculture industry and/or which are diseases listed by EU or WOA (World Organisation for Animal Health, founded as OIE). Millane et al. (2019) screened pink salmon captured in Ireland and found all negative for infectious salmon anemia virus (ISAV,  $n=13$ ), *Renibacterium salmoninarum* Micrococcaceae ( $n=13$ ) and salmonid alphavirus (SAV,  $n=15$ ). Thus far, information available on the health and infection status of pink salmon in Norway exists outside of the peer-reviewed literature Skjåvik (2008) examined 38 pink salmon from River Tana and 36 from River Neiden in 2007 and did not detect any of the screened viruses which included infectious hematopoietic necrosis virus (IHNV), infectious pancreatic necrosis virus (IPNV) or ISAV. Fjær (2019) examined 40 pink salmon from River Etne in 2017 and did not detect the viruses SAV, IPNV, piscine myocarditis virus (PMCV), IHNV, or PRV (genogroup not specified). The Institute of Marine Research in Norway detected ISAV in two of 40 pink salmon captured in River Etne in 2017 (Kvamme et al., 2018). Due to low viral load, it was not possible to sequence the PCR product to decide whether it was a non-virulent (HRP0) or virulent (HRP-deleted) variant. Rullestad (2021) investigated the occurrence of parasites and selected viruses in 86 pink salmon caught at sea during the period 2013–2019. The Norwegian Veterinary Institute did not detect ISAV, *R. salmoninarum*, IHNV or VHSV in the 2019 and 2021 surveillance programs (Garseth, Florø-Larsen, et al., 2020; Garseth, Gåsnes, et al., 2020; Garseth et al., 2022). However, in 2019, high viral loads of PRV-1b were detected in pink salmon captured in River Karpelv, Finnmark (Garseth, Florø-Larsen, et al., 2020; Garseth, Gåsnes, et al., 2020). This is the genotype that is associated with heart and skeletal muscle inflammation (HSMI) in Atlantic salmon (Garseth, Florø-Larsen, et al., 2020; Garseth, Gåsnes, et al., 2020). PRV has previously been detected in pink salmon in the Pacific Ocean (Purcell et al., 2018) PRV-1 [unknown subtype] and has since been detected in pink salmon captured in several other rivers and in the

sea in Norway (Garseth, Florø-Larsen, et al., 2020; Garseth, Gåsnes, et al., 2020; Rullestad, 2021). Further surveillance and monitoring of invading pink salmon in the North Atlantic will continue to provide information. Furthermore, experimental transmission studies of selected pathogens (SAV, ISAV) can provide important information.

### 2.3.3 | Immunosuppression, increasing host density and impact on infection dynamics

Semelparity makes reproduction the primary investment as pink salmon end their marine migration. At this stage, pink salmon undergo complex and comprehensive changes to maximize spawning success. They stop feeding, the digestive tract atrophies, and energy is allocated to gametogenesis, development of secondary sexual characteristics, shift of osmoregulation, nest digging and defence in females, and courting of females in males (Carruth et al., 2002; Cook et al., 2011; Dickhoff, 1989). Elevated neuroendocrine functions result in suppressed immune functions, increasing the susceptibility to infections (Cook et al., 2011; Dickhoff, 1989). Immunosuppressed, moribund and dead and decaying pink salmon may also have an impact on the microbial balance in rivers by being easy targets for more opportunistic bacteria that are naturally present in the environment and in fish skin, gills and intestines. For instance, haemorrhagic septicemia due to the opportunistic bacteria *Aeromonas hydrophila* Aeromonadaceae was diagnosed in a female pink salmon that was found dead prior to spawning in River Gjørsjøelva in Norway in 2021 (Garseth, Florø-Larsen, et al., 2020; Garseth, Gåsnes, et al., 2020). *Aeromonas hydrophila* is ubiquitous but can act as a primary pathogen when host density is high. The bacteria can cause disease in fish, amphibian, reptile and human hosts (reviewed in Aoki, 1999). From a fish health and one-health perspective, research on how large numbers of immunosuppressed, moribund, or dead and decaying pink salmon affect the riverine microbiota is recommended.

## 2.4 | Staging, spawning and death

### 2.4.1 | Selection of spawning territory

In rivers draining to the Pacific Ocean, pink salmon may arrive first on spawning grounds and reproduce earlier than other salmonid species (Essington et al., 2000, but see Fukushima & Smoker, 1998). Pink salmon being smaller than other salmon should drive a preference for spawning in smaller substrates that they can more easily excavate, however, the few investigations of habitat segregation between pink salmon and congeners in the Pacific do not provide compelling evidence for this. Pink salmon tend to spawn at the tail of pools in Pacific rivers. Fukushima and Smoker (1998) suggested pink salmon spawned in shallower, steeper and faster flowing reaches than sockeye, but stopped short of concluding that this was a preference. Nelson et al. (2015) suggested pink salmon spawning density was negatively related to riparian slope and positively related



to woody debris in the river. Ultimately, pink salmon appear to pick spawning areas where interstitial gravel is well-oxygenated.

Despite exceptional habitat mapping of substrate size and type in many Norwegian rivers, to determine habitats available for native salmonids, there is not yet any mapping of pink salmon spawning redds. However, Erkinaro et al. (2022) found pink salmon spawning in swift water near shorelines with gravel substrate in the Tana/Teno River system that spans the Norway/Finland border. Bjerknes and Waag (1980) provide some early descriptions of pink salmon spawning in northern Norway and suggest limited interference of the pink salmon spawning on Atlantic salmon that spawn over a month later. However, the timing of pink salmon spawning in northern Norway may undergo rapid selection to increasingly overlap with the native species. Spatially, Vistnes (2017) and Sørvik (2022) observed that pink salmon in some cases spawned closer to the river banks than Atlantic salmon, and in 2–32 mm gravel size. Alekseev et al. (2019) found that pink salmon and Atlantic salmon spawned in close proximity but Atlantic salmon spawned in slightly deeper areas. It is not clear if this is due to preferences on the part of the two species, or resulted from competitive interactions. Although there are reports of pink salmon spawning in shallow water, and to some extent in finer gravel than Atlantic salmon, there are observations of common spawning areas between Atlantic salmon and pink salmon in several Norwegian rivers (Anon, 2022a, 2022b; Hansen & Monsen, 2022; Muladal & og Fagard, 2020, Muladal & og Fagard, 2022; Sørvik, 2022; Vistnes, 2017). Risk of redd superimposition for pink salmon should be high in areas where their conspecifics in the Pacific are also spawning given the chronology of the spawning window, although pink salmon may dig relatively deep redds for their size (Scott & Crossman, 1973). In the native range, high abundance of pink salmon will lead to superimposition, meaning early spawning fish will have much lower spawning success; this suggests that in European rivers newly colonized high numbers of pink salmon, the colonizing fish might have undergone strong selection historically against early spawning (Esin et al., 2012). Essington et al. (2000) found no effect of later-spawning sockeye salmon abundance on the productivity of pink salmon in Weaver Creek of the Fraser River, suggesting limited redd superimposition. Pink salmon may be adapted to finding spawning areas where competitors will not readily excavate them. Pink salmon juveniles have even been found together with eggs of Atlantic salmon, and the pink salmon have seemingly had a high survival even though the Atlantic salmon must have been spawning in the same redd after the pink salmon have spawned (Hansen & Monsen, 2022; Muladal & og Fagard, 2020, Muladal & og Fagard, 2022). Thus, it is not clear whether or not the superposition of late-spawned Atlantic salmon redds over earlier spawned pink salmon redds will have a significant effect on the ability of pink salmon to colonize new watersheds.

#### 2.4.2 | Temperament on spawning grounds

Pink salmon are aggressive on spawning grounds (Figure 6-3; Quinn, 2018). Males are mostly aggressive towards other males but

females are aggressive towards both males and females including other species (Quinn, 2018). Keenleyside and Dupuis (1988) observed aggression by dominant males towards other females and by females during the spawning season as part of their efforts to maintain dominance and maximize reproductive success. Few accounts of pink salmon aggression towards heterospecifics are available and few observations have been described in the weeks prior to spawning. However, there is evidence that the pink salmon may be directly or indirectly responsible for displacing Atlantic salmon from their preferred holding places (E. Frøiland, pers. comm.). Displacement from optimal holding areas may have negative impacts on Atlantic salmon, especially if it causes aggregation of a large number into smaller areas of a river where they are prone to thermal stress, predation, energy depletion, pathogen transmission, or poaching. Any such impacts of pink salmon on native species would affect angling opportunities, satisfaction and economic capitalization of this important economic sector in European rivers where salmon fishing is culturally ingrained (Guay, 2022). Local managers and fishers in several Norwegian rivers have reported that they have observed that Atlantic salmon seem to stay away from pink salmon spawning areas during the spawning period (observations from land in clear water rivers, and by snorkeling surveys, e.g. Anon, 2022a, 2022b; Sørvik, 2022; Vistnes, 2017). They have also reported that pink salmon of both sexes become increasingly aggressive towards other fish during the spawning period and that male pink salmon may move extensively on the spawning grounds whereas the females remain to a larger extent near the spawning redds. Male pink salmon may be more aggressive towards other fish before spawning, whereas females seem to be more aggressive in the period after spawning. More direct observations of interactions between pink salmon and Atlantic salmon using snorkelers or video recordings can help understand these dynamics better. Tracking Atlantic salmon in years with and without pink salmon using activity sensors may also help determine whether Atlantic salmon are exposed to excess energy demand due to aggressive interactions in odd-numbered years when they co-occur with pink salmon.

#### 2.4.3 | Attraction of predators

Pacific salmon are a major resource subsidy to the terrestrial environment. Grizzly bears (*Ursus arctos*) and black bears (*Ursus americanus*) stand in rivers and catch salmon and wolves (*Canis lupus*) are major beneficiaries of the seasonal salmon runs within their range (Adams et al., 2010). Piscivorous wolves are currently not seen in Norway and polar bears (*Ursus maritimus*) are rare and confined to the most northerly areas, but eagles, foxes and otters are common riparian predators that stand to be major beneficiaries of increased salmon abundance in their area. In Patagonia, Muñoz et al. (2022) summarised several important biological responses to the Chinook salmon invasion, including subsidies of scavengers such as rodents, invasive mink and the culepo fox (*Lycalopex culpaeus* Canaidae). Otters (*Lutra lutra* Mustelidae) have recently

recolonized much of Norway following historic extirpation and are generating conflicts with local fishing organizations and aquaculture; they are a predator of Atlantic salmon in Norway, but their exploitation of pink salmon is not known. Marine mammals, especially seals in coastal zones (*Phoca vitulina* Phocidae) can feed on Atlantic salmon (Butler et al., 2006) and in the Pacific they are believed to exploit pink salmon migration (Zamon, 2001). Indeed, Lance et al. (2012) found that salmonids comprised more than half the diet of harbour seals in Puget Sound, with the contribution most pronounced in odd-numbered pink salmon years. Not only will direct predators be affected by pink salmon, but scavengers of adult carcasses such as foxes (*Vulpes vulpes* Canidae) and white-tailed sea eagle (*Haliaeetus albicilla* Accipitridae) will likely benefit from the additional food in odd-numbered years and enjoy increased reproductive success.

The impacts of pink salmon on the predator and scavenger community in coastal and riparian zones are predicated on much speculation, and research is clearly needed to understand how these dynamics will unfold in the novel range of the pink salmon. We predict that pink salmon has the potential to support an expanded predator and scavenger community and therefore increased abundance of piscivorous mammals and marine fish that can exploit abundant pink salmon and improve their reproductive success in odd-numbered years. In even-numbered years when pink salmon are not abundant, we predict that this subsidized predator community will have to switch to native species to persist in the absence of its primary supporter; therefore, Atlantic salmon, brown trout and Arctic charr may experience increased attack rates from an expanded predator community. The potential for increased human-wildlife conflicts in even-numbered years is predicted to be high, and we submit that this should be a priority for new evaluations and research into the socioecological impacts of pink salmon on coastal communities, ecosystems and economies.

#### 2.4.4 | Nutrient loading from carcasses and eggs

Pacific salmon die after spawning and release a substantial nutrient pulse into rivers where they have spawned; these nutrient pulses are iconic in the Pacific and have inspired many studies into the ecosystem responses of the eutrophication derived from salmon carcasses in rivers (Moore et al., 2007; Quinn et al., 2018). Some Atlantic salmon rivers are contemporarily suffering from oligotrophication due to barriers and land-use changes that have limited the transport of nitrogen and phosphorus from headwaters to stream channels (Bernthal et al., 2022). Consequently, the arrival of pink salmon in such rivers may increase stream productivity and the growth of native salmonids and provide an alternative to proposals that have suggested artificial addition of nutrients to enhance stream productivity (e.g. Williams et al., 2009). Indeed, pink salmon spawning runs were found to increase the nutrient loading in Great Lakes tributaries, even with relatively small runs (Schuldt & Hershey, 1995).

In the Pacific area, pink salmon eggs are eaten by juvenile coho (*Oncorhynchus kisutch* Salmonidae) and confer a growth advantage

(Nelson & Reynolds, 2015) that may be reflected by native parr in the Atlantic (Rasputina et al., 2016). Indeed, Dunlop, Wipfli, et al. (2021) confirmed that juvenile Atlantic salmon in northern Norway were profiting from marine-derived nutrients patriated by Pacific salmon to their home rivers. Given the massive number of fish (Atlantic salmon predominantly) scales that are delivered by recreational fishers in Norway each year, it will be possible to test whether juvenile salmon enjoy improved growth in synchrony with the biennial peak in nutrients from pink salmon invasions. Such measurements can be taken by either measuring growth increments of the scales or extracting isotopic information to search for marine nutrient enrichment in alternating years.

In some cases, excess nutrients patriated by pink salmon may result in a biological oxygen demand in the river and a variety of subsequent and sometimes negative consequences for the river ecosystems, such as increased macrophyte growth, pathogen and fungal propagation, and hypoxia. In the Atlantic and Pacific, anadromous fish carcasses have been documented to support proliferation of biofilm (Harding et al., 2014; Samways et al., 2015). Moreover, experiments suggest that Atlantic salmon carcasses (or their analogues) confer an advantage to alevins from large eggs and with high metabolic rates (Auer et al., 2018). Nutrient loading from pink salmon correlates with biofilm growth in the Pacific (Harding et al., 2014), but there is no clear evidence that the nutrients introduced by decomposing salmon have any negative impacts in the native range. It is also possible that unanticipated impacts could occur to terrestrial systems in areas where pink salmon are invading, especially in the North where food is limited and food chains short. For example, at Svalbard streams are at risk of colonization by pink salmon (Witkowski & Głowacki, 2010). The presence of the species would provide a seasonal food source for polar bears.

For Atlantic salmon, brown trout and Arctic charr, which are still preparing to spawn when pink salmon die, there may be risks posed by the decomposition of pink salmon carcasses. Atlantic salmon and Arctic char frequently are wounded during redd digging and aggressive interactions pre-spawning, and infection risk to these wounds could become elevated if the decomposing carcasses stimulate the spread of pathogenic organisms. Bjerknes and Waag (1980) first suggested that the preponderance of pink salmon may aggravate production of fungus that spills over to wild salmonid eggs where their spawning grounds overlap, but no subsequent investigations have been made. Fungal infections are considered to be a factor in post-spawning mortality of iteroparous salmonid kelts. Consequently, there may be poorly understood but significant consequences of eutrophication for these species if pink salmon carcasses support proliferation of pathogenic species.

#### 2.4.5 | Introgression and hybridization

Notwithstanding separation of spawning times, captive assessments of the potential for hybridization of pink salmon with Atlantic salmon have concluded that pink salmon crossed with Atlantic salmon do not produce viable embryos (Ban et al., 2013; Loginova & Krasnoperova, 1982) or reach sexual maturity (Devlin et al., 2022).

The same holds true for pink salmon crossed with brown trout and Arctic charr. Introgression of pink salmon with native salmonids is not considered a risk (Hindar et al., 2020).

### 3 | DISCUSSION

Pink salmon is clearly positioned to be a climate winner in temperate and sub-Arctic oceans. Relatively small and short-lived and plastic in their feeding habits, pink salmon are excellent colonizers, buoyed by a lower affinity for natal rivers than other more philopatric salmonids. Such low affinity has led the species to transition from the White Sea populations where it was stocked in Northwest Russia to Norway, Ireland, Scotland, Iceland, soon elsewhere in Europe including potentially the Baltic Sea, and across the Atlantic to Canada. Similar transitions were observed in the Laurentian Great Lakes, where the species successfully colonized the four other lakes following introduction to Superior (Lee, 1981). Pink salmon are, in many ways, a fish of the future in the north Atlantic; one that can tolerate warm temperatures, shift its range in response to climate change, and mature quickly to avoid prolonged exposure to a variable marine climate (Clark et al., 2011). The consequences of this invasion in the Atlantic and Arctic Oceans for native species are yet to be revealed, and we consider this to be a high-priority research area in both marine and freshwater sciences (Box 1).

We predict that pink salmon, if occurring in large numbers in the Atlantic and Barents rivers, will impact the behaviour of adult Atlantic salmon, sea-run brown trout and Arctic charr during river entry, upstream migration, and holding before spawning, which may result in reduced reproductive success of native salmonids, and in reduced angling opportunities, which is important for local economies. Pink salmon may also disturb the spawning of Arctic charr and the earliest spawning brown trout—and over time, evolve into spawning later in the season and thereby pose a greater risk of disturbing the spawning activity of Atlantic salmon. We further predict negative impacts by pink salmon juveniles on juvenile stages of native salmonids through overcrowding and possible food competition in the spring and early summer. Nutrient loading from pink salmon carcasses in the rivers may lead to increased growth of native salmonid juveniles, with unpredictable outcomes; and in worst case, smolting at a younger age and size and subsequent lower marine survival. Overall, a large pink salmon population may reduce the production and abundance of Atlantic salmon, sea-run brown trout and Arctic charr in a river. On the ecosystem scale, pink salmon can alter river ecosystems and impact cycles of terrestrial mammals and birds and their prey. In the ocean, we know from the Pacific that pink salmon in large numbers can impact abundance and cycles of other marine fish, birds and mammals, and although we predict that pink salmon abundance is far from reaching such high levels in the Atlantic Ocean, we are at present more worried about the potential

#### BOX 1 Research priorities for pink salmon in three oceans.

##### Research Priorities



Given the state of knowledge in the Pacific realm and the emerging research in the Arctic and Atlantic, there is a clear need for a comprehensive research effort to understand pink salmon in the three oceans. From our review, we present the following research questions among the most urgent to address and the most uncertain:

1. Will pink salmon contribute to eutrophication of estuaries in northern rivers?
2. Will pink salmon subsidize predator communities in alternating years, creating excessive pressure on native species in years when pink salmon are relatively scarce?
3. Will pink salmon contribute to regime shifts in the Atlantic or Arctic Oceans?
4. What is the evolutionary potential of pink salmon confronted by climate change?
5. What is the theoretical distributional freshwater limit of pink salmon in the Atlantic?
6. How large is the impact of pink salmon aggression on native species?
7. Will pink salmon spread pathogens to native species or to fish farms?
8. Will pink salmon proliferate fungus or bacteria in rivers that affect native migrants during migration, spawning, or overwintering?
9. How will fishers and fisheries adapt to account for the impacts of pink salmon on ecology and economy?
10. Will management systems resist, adapt to, or direct the invasion of pink salmon?

impact on other species in estuaries, fjords, and near-coastal areas, where pink salmon locally may occur in large densities already now or in the near future. We also predict that pink salmon will interact with native salmonids and fish in aquaculture farms through transfer of pathogens, but in unpredictable ways. Their return migration pattern along large parts of the Norwegian coast, as seen in 2021, may allow for interactions between individual pink salmon and several aquaculture farms along the migration route and allow for transfer of pathogens over large distances. Finally, we hypothesise that the pink salmon in large numbers may deteriorate the water quality in watersheds, with consequences for drinking water quality and recreational activities. At present, these predictions are not supported by existing knowledge due to the lack of studies, leading to the urgent need for solving the research questions listed in [Box 1](#).

By reviewing literature on the life history, behaviour and physiology of pink salmon in its native range, we were able to reveal several vulnerabilities of the Arctic and Atlantic to the pink salmon invasion. Despite little research having been conducted directly on pink salmon in Russia, Norway and other Atlantic countries, several nations have conducted risk assessments (Armstrong et al., 2018; Hindar et al., 2020; Millane et al., 2019; Sandlund et al., 2019). Data regarding where and when pink salmon reproduce in Atlantic rivers have not been systematically mapped and overlaps in space and time with native salmonids is therefore not yet fully documented despite a general observation that native species have tended to be spawning later and in deeper redds than pink salmon. Interference competition among pink salmon and native Pacific salmonids seems to have been attenuated by evolution of the species (although not eliminated; Ruggerone & Nielsen, 2004), however, a lack of shared evolutionary history between pinks salmon and Atlantic salmonids suggests the potential for direct interference in rivers where they overlap in time and space especially on or around spawning grounds.

Millions of pink salmon smolts entering coastal areas in the Atlantic may exert significant local impacts on food webs and offer an opportunity to scientists to conduct natural experiments as the pink salmon fluctuate in abundance between odd and even numbered years. Large nutrient pulses emanating from rivers to fjords, lochs and coastal zones are likely to attract predators and enhance growth for fish that are able to exploit the smolt run, which may enhance pressure on native species in every other year when pink salmon are less abundant. Marine predators like cod, saithe (*Pollachis virens* Gadidae) and sea-run brown trout that feed on Atlantic salmon smolts exiting rivers in springtime may switch between pink and Atlantic salmon smolts from year to year, depending on the availability of pink salmon. Isotopic methods provide a promising method for demonstrating the trophic pathways in rivers that pink salmon have started to influence in Norway (Dunlop, Wipfli, et al., 2021), and there is potential for similar pathways to be investigated in other Atlantic coastal waters as well.

Arctic ecosystems are relatively fragile with endemic species adapted to the extreme conditions. Pink salmon are beginning to appear in the Arctic, with observations of pink salmon feeding in

fjords of Svalbard and Greenland and even attempting to migrate up rivers in Svalbard to spawn (Witkowski & Głowacki, 2010). There are relatively few fish in the high Arctic marine environment but pink salmon may become one of the first species to penetrate the Fram Strait into the Arctic Ocean. If pink salmon from continental Europe begin to feed in the high Arctic, impacts on the food web are unpredictable. Polar cod (*Boreogadus saida* Gadidae) forms the base of the food web for seabirds and marine mammals in these northern areas (Hop & Gjørseter, 2013) and penetration of Atlantic species as competitors has the potential to influence these sensitive ecosystems in currently unpredictable ways. For rivers in Greenland and Svalbard, should pink salmon attempts to spawn be successful, it may result in dramatic shifts in the productivity of cold, unproductive rivers used predominantly by Arctic charr.

A focal point of future work on invading pink salmon should be understanding not simply the mean timing but the variation and the potential for selection to operate on key life history aspects of the species sculpting phenotypes towards a viable, productive, and potentially dominant species in the Atlantic arena (Beacham, 1988; Gordeeva & Salmenkova, 2011). Pink salmon not only altered their migratory phenotypes when they established in the Great Lakes, but their genetic composition changed signalling evolution of the population (Gharrett & Thomason, 1987). Comparing pink salmon in the introduced Russian population and the source Magadan population of northern Russia, Gordeeva and Salmenkova (2011) found that the introduced pink salmon in western Russia had larger weight at size and higher fecundity than the original population, confirming selection and heritable changes to the population following transplantation. Important changes to phenology and life history were also observed, including later fry migration, and average size at maturity has increased from 1.3 to 1.9 kg during the last decade (Citing Veselov in Hindar et al., 2020).

Present concerns about the trajectory of pink salmon in the North Atlantic are tempered by speculation that the species is not well adapted to the existing temperature regime and overall environment. However, this may change rapidly both due to the changing environment and natural selection of the colonists if there is sufficient trait variation and heritability of these traits to generate selective gradients fostering adaptation to conditions in southern Norway and elsewhere in Europe. The level of genetic variation has been suggested as one reason why the more genetically variable odd-year population in the White Sea has been more successful than the even-year population (Gordeeva et al., 2015). Time lags in the invasion are expected; establishment in Lake Superior, and eventual spread to all four other Laurentian Great Lakes, took several generations. The first six generations of pink salmon stocked in Superior produced marginal returns but by the eighth generation, pinks were suddenly widespread in tributaries of the lake (Wen-Hwa & Lawrie, 1981). Is it simply a matter of time before the Atlantic and Arctic pink salmon populations make a similar leap?

Pink salmon are clearly a plastic species and assumptions about their ecology should not only be made based on knowledge



from the Pacific realm or even from accounts of the species in the western Russian source population. Relative to other salmonids, knowledge about pink salmon is relatively less well developed and communicated given their lower economic value compared to Atlantic, chinook, sockeye, coho and other salmonids. Yet, the pink salmon is a fascinating species that is likely to be a winner from climate change. We suspect pink salmon are already in the midst of rapidly adapting to its new habitats in Europe. At present, pink salmon in the Atlantic are following a cyclical pattern of abundance where they are returning to rivers to spawn in odd-numbered years, but the future may include a greater representation of even-numbered year classes as well. For now, the cyclic abundance provides a unique lens through which to study the invasion to develop new knowledge about the species and its impacts in a natural experiment with control and treatment years (e.g. Brown et al., 2020).

This paper is being written at the end of 2022 as we prepare for a suspected mass influx of pink salmon to European rivers in summer 2023. Our level of knowledge about the species remains poor. By the end of the decade, we may see an historic change in river ecologies in northern Europe, especially northern Norway and Finland but potentially also in Baltic countries if pink salmon continue to spread and adapt (Staveley & Bergendahl, 2022). By 2030, we suspect pink salmon will be regularly interacting with native species in rivers and exhibit adaptive changes from source populations in key life history traits and phenology. Given the projections for further warming in the North Atlantic and in the rivers that pink salmon are already increasingly colonizing in Europe, pink salmon are projected to be a climate winner, and in the next decade, we anticipate a much broader spread of the species within the Atlantic Basin. Although pink salmon abundance fluctuates quite a lot in the Pacific over many years, making it difficult to predict the abundance in each year, our prediction is that the long-term trajectory of pink salmon in the Atlantic will be a very significant increase in abundance. Systematic scale or otolith collection, as well as genetic sampling, will be key to develop a time series to investigate growth of pink salmon and genetic changes throughout their novel distribution. Moreover, there is great opportunity to use scales from native Atlantic salmon to investigate how biennial changes in nutrient fluxes from pink salmon influence Atlantic salmon early life growth and how food competition with pink salmon while the species are at sea affect the survival and growth of adult Atlantic salmon. We hope that by the end of the decade that management plans for pink salmon have been installed and that conservation of native Atlantic salmon, Arctic charr and brown trout is assured in highly affected rivers. As invasive species become increasingly problematic in coming years, we suspect that the expansion of pink salmon will become one of the most consequential biological invasions to ever affect North Atlantic marine ecosystems. This argues for immediately focusing major research efforts on the issue to understand how these ecosystems will change, how we could adapt our management and policy regimes to cope with the consequences of the changes, and to derive lessons on how we might avoid similar undesired invasions in the future.

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## DATA AVAILABILITY STATEMENT

Data are available on [Zenodo.org](https://zenodo.org).

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